EXAMINATION AND COMPARISON OF MANDIBLES AND GASTRIC MILL TEETH IN TWO SPECIES OF CRAYFISH, *Procambarus alleni* (FAXON) AND *Procambarus fallax* (HAGEN) THAT INHABIT EVERGLADES WETLANDS

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Introduction

Crayfish are considered to be one of the most important groups of freshwater animals found in aquatic ecosystems, where they serve as keystone species and have an important biological impact on primary producers and consumers (Holdich 2002) that influences all community trophic levels (Lorman and Magnuson 1978; Jordan 1996). As one of the most important groups of freshwater omnivores (Hobbs 1993), their diet includes living plant tissues, detritus, and a variety of animal prey (Cronin 2002).

Research on structure and function of masticatory structures in decapod crustacaeans has been conducted on the influence of diet and phylogeny (Caine 1975 a, b; Bouchard 1977; Meiss and Norman 1977; Suthers and Anderson 1981; Suthers 1984; Chikasa and Kozawa 2003). Much of the research was focused on the structure and function of mandibles and the gastric mill complex. Differences in mandibles and gastric mill teeth were found between epigean (above-ground dwelling) and hypogean (cave-dwelling forms) crayfish (Caine 1975a). Feeding structures of epigean procambarids were more complex than those of hypogean forms of procambarids.

Little research has been conducted on feeding habits of *Procambarus alleni (Ev*erglades crayfish) and *P. fallax (*Slough crayfish) (**Figure 1)**, but it is apparent that there are some differences between the species that can account for microhabitat differentiation. Everglades crayfish prefer temporary aquatic habitats and are known to migrate and burrow, whereas Slough crayfish are more likely to inhabit permanent bodies of water probably containing aquatic vegetation year-round (Rhoads 1970; Hendrix 2000; VanArman 2003). However, both species have found living in syntopic distribution in the Corbett Area (VanArman 2003), as well as in more southern Everglades wetlands (Hendrix 2000). Availability of food in the natural environment, differences between types of feeding; and phylogenetic influences may account , in part, for different microhabitat usage.

Epigean procambarids have similar functions and structures of feeding anatomy (Caine 1975a; Chikasa and Kozawa 2003). The focus of this study is to determine if there are differences in feeding anatomy between the two South Florida species, by examining mandibles and part of the gastric mill complex (median and lateral teeth) in the foregut. Mandibles and the gastric mill complex median and lateral teeth were examined for structure, size (length and width) and numbers of mandibular and lateral teeth . The overall (null) hypothesis is that there will be no significant differences between Everglades and Slough crayfish with regard to these parameters. Differences will be considered significant for any of these structural comparisons if $p \leq 0.05$. Significant differences in size or structure of mandibles or gastric mill features will be discussed in relation to habitat, behavior, diet, and implications for Everglades restoration.

Materials and Methods

Collecting sites:

Crayfish were collected, using minnow and crayfish traps and dip nets, from December 2007 through March 2008 at Big Pine Key (Florida's Keys--Monroe County), Sanibel Island (Florida's south west coast --Lee County), J. W. Corbett Wildlife Management Area (Corbett) and Grassy Waters Nature Preserve (GWNP-Palm Beach County) **(Figure 2)** . The latter two sites are part of the historic Everglades. Traps were set up in natural areas overnight.

Methods:

In the laboratory, each crayfish was identified to species and gender, weighed, and measured for total length, orbital carapace length, and carapace width with a vernier caliper following standard procedure (**Figure 3)** (Bovbjerg 1953, 1956; Austin 1995; VanArman 2003). Rostral and orbital lengths were measured to account for inaccuracies presented in case of stubby or broken rostra. Crayfish were then preserved in 70% ethanol in individual 4 oz screw top specimen jars.

Mandibles:

Study of mandibles began by removing tissue from the area surrounding the mandibles and noting mandible orientation (overlap of one mandible on the other). The carapace was broken to expose the mandibles for measurement and photography. The length of each mandible was measured from the lateral point of connection with the body to the tip of the longest incisor, generally the largest and longest tooth found at the anterior edge of the gnathal lobe **(Figures 4,7a, b).** The gnathal lobe was measured across its widest point just behind the teeth. Measurements were taken with Vernier calipers. The number of teeth was determined by counting the separate ridges and peaks on the outermost curvature of the gnathal lobe.

Gastric mill teeth:

Crayfish cardiac stomachs (**Figure 5)** were removed by peeling the carapace and cutting the stomach from the anterior part of the body. Gastric mill teeth were separated from the stomach under a Leica dissecting microscope. The median and lateral gastric mill teeth (**Figure 6a)** were then photographed with a Sony digital camera at magnifications of around 20-35x. Shape, structural arrangements, length of median teeth, width of the mesocardiac ossicle at its widest point, width of the lateral teeth plate and number of teeth on each right and left lateral tooth plate were recorded.

Statistical analysis:

Statistical analysis of data was based on an independent samples t-test, not assuming equal variance, using SPSS 14.

a. Size of tested crayfish: The first test was made to determine whether there was a significant difference in total length between test specimens of both species.
b. Mandibles: To determine significant mandible differences between species, data from the values of length and width of right and left mandibles and number of teeth on each mandible were analyzed.
c. Gastric mill complexes (median tooth, lateral teeth): To determine if significant differences of the gastric mill complex median and lateral teeth) existed between species, the length of the gastric mill median tooth and width, of the mesocardiac ossicle, the length and width of lateral teeth plates, as well as number of teeth on each plate were compared.

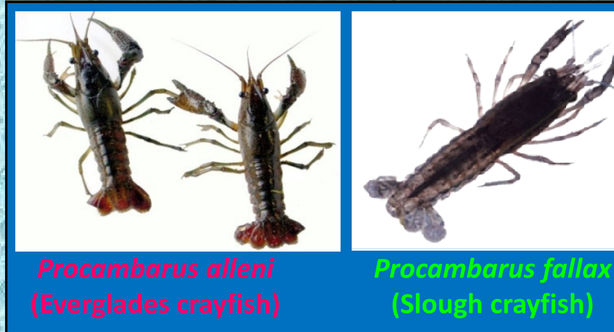

Figure 1. Everglades and Slough crayfish

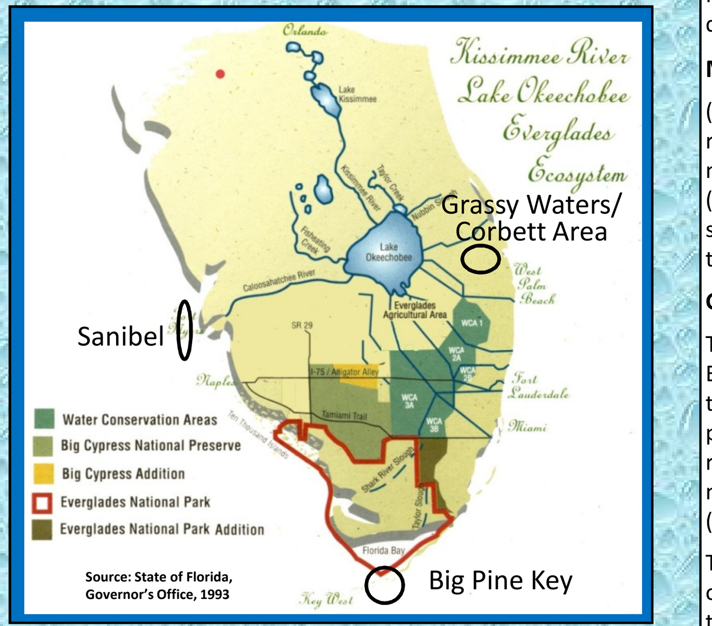

Figure 2. Locations of areas where crayfish were collected

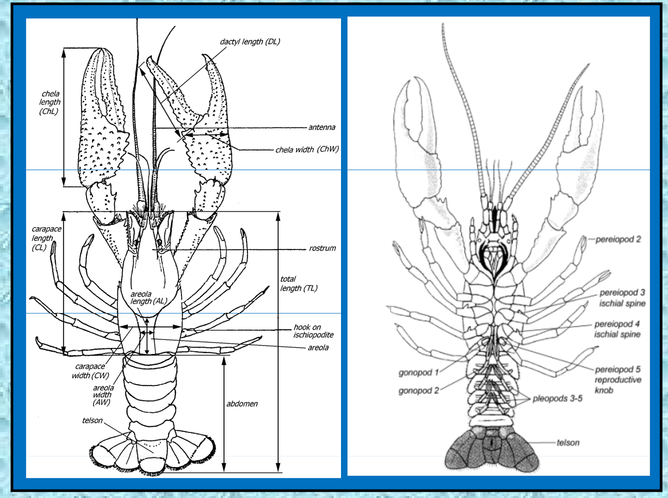

Figure 3. Major features of crayfish and measurements used in this study

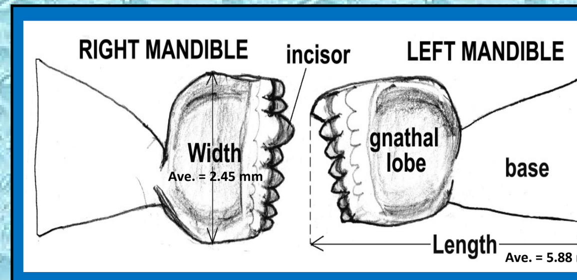

Figure 4. Ventral View of Mandibles of Pa

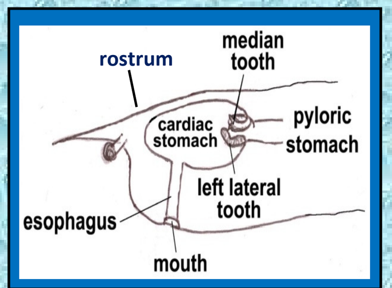

Figure 5. Internal anatomy of the digestive tract – location of gastric mill teeth

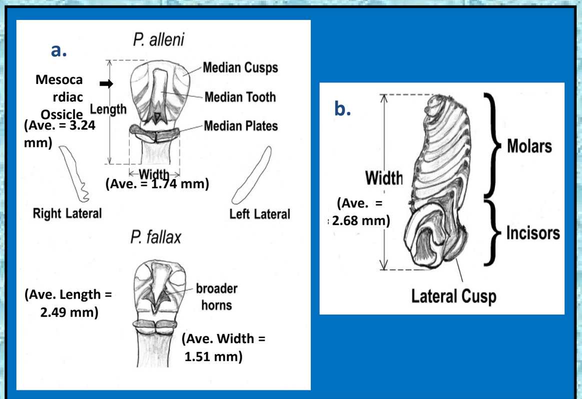

Figure 6. a. gastric mill teeth of Pa and Pf. b. ventro-medial view of left lateral tooth of Pa

Results

Size of Crayfish:

Table 1 shows results of statistical tests that showed significant differences in the measured parameters between species. Initial test s were made based on sizes of the specimens examined. *P. alleni,* in general are larger than *P. fallax.* This difference in size was reflected in the "all data" set for crayfish collected (hypothesis 1a in **Table 1**). The second test was to determine whether there was significant difference in the sizes of the crayfish between those specimens of the two species of crayfish that were actually measured, the "complete data" set (hypothesis 1b in **Table 1**). Results indicated that the specimens of the two species used in this analysis did not differ significantly (p=0.486) from each other with respect to size.

Mandibles:

(**Figures 4, 7a and 7b**) Slough crayfish had significantly more teeth on the right mandible (pa=7.43 teeth, pf=8.29 teeth) (p=0.030) and on the left mandible (pa=5.76 teeth, pf= 6.94 teeth) (p<0.001), than Everglades crayfish (**Table 1**). The mean number of teeth on the right mandible (7.82 teeth) significantly exceeds (P<0.001) the mean number of teeth on the left (6.29 teeth), regardless of species.

Gastric mill complex:

The length of the median tooth on the mesocardiac ossicle (**Figure 6a**) of the Everglades crayfish (3.24 mm) was significantly longer (p=0.008) than the tooth (2.49 mm) of the Slough crayfish .The right and left lateral teeth plates of Everglades crayfish were significantly (p=0.015 and 0.025, respectively) wider (2.66-2.68 mm) than those of Slough crayfish (2.09-2.10 mm). Slough crayfish have significantly more teeth on lateral plates (p=0.036).

The median tooth in the gastric mill of Everglades crayfish is longer than that of Slough crayfish, but not wider. In both species, the dorsal projection of the median tooth is "Y' shaped with the stem of the "Y" fixed to the mesocardiac ossicle (**Figures 6a, 7c, d**). The pointed arms of the "Y" are blade- shaped with thin sharp margins and a thicker center. However, the median tooth of Everglades crayfish appears to be more slender, and has arms that are more pointed and extend ventrally. The dorsal projections of the median tooth of Slough crayfish seem to be broader, point laterally, and appear more wing-like.

The lateral teeth of both species looked similar. Each lateral tooth contained four incisors, and the remainder of teeth were molars (**Figure 6b, 7c,d**). Lateral teeth plates are wider on Everglades than Slough crayfish. Within a given species, the number of teeth on left and right lateral tooth plates is the same, but Slough crayfish have significantly more teeth on the lateral plates than Everglades crayfish.

Table 1. Results of Statistical analyses of differences among selected morphological features *of Procambarus fallax* (Pf) and *Procambarus alleni* (Pa)

Body Size

Hyp. No.	Parameter	Mean (Pa)	N (Pa)	Mean (Pf)	N (Pf)	t	df	P	Reject H_o?	Conclusion
1a	all data" set mean total length	59.94	42	50.64	42	3.494	65.486	0.001	yes	Pa>Pf
1b	"complete data" set mean total lengths	54.17	21	50.79	17	0.704	33.647	0.486	no	Pa NSD from Pf

Mandibles (based on "only complete data" set – 38 specimens)

Hyp. No.	Parameter	Mean (Pa)	N (Pa)	Mean (Pf)	N (Pf)	t	df	P	Reject H_o?	Conclusion
5a	Mean no. of teeth on right mandible	7.43	21	8.29	17	2.226	35.674	0.030	yes	Pf >Pa
5b	Mean no. of teeth on left mandible	5.76	21	6.94	17	3.970	24.299	0.001	yes	Pf >Pa
5c	Both species combined, mean no. of teeth on right (R) and left (L) mandibles	Mean (R)	N (R)	Mean (L)	N (L)	5.795	71.590	<0.001	yes	Right > Left
		7.82	38	6.29	38					

Gastric Mill Teeth (based on "only complete data" set – 38 specimens)

Hyp. No.	Parameter	Mean (Pa)	N (Pa)	Mean (Pf)	N (Pf)	t	df	P	Reject H_o?	Conclusion
6a	Mean length of gastric mill tooth	3.24	21	2.49	17	2.830	35.682	0.008	yes	Pa >Pf
7a	Right Lateral Tooth width	2.68	21	2.09	17	2.369	27.281	0.025	yes	Pa >Pf
7b	Left Lateral Tooth width	2.66	21	2,10	17	2.369	27.281	0.025	yes	Pa >Pf
8	No. Teeth on Lateral Plates	13.9	21	15.4	17	2.405	27.281	0.036	yes	Pf>Pa

Discussion

Since both Everglades and Slough crayfish can live in close proximity to one another (e.g. the two species were captured together in the same traps in the Corbett area), it seems likely that some degree of microhabitat partitioning may be occurring. Differences in feeding structures between the two species, especially when combined with behavior and habitat preferences, may indicate that they are consuming different primary food sources. Observations by the authors on both species of crayfish in natural areas, as well as under laboratory conditions, show that Everglades crayfish are more aggressive than Slough crayfish. Laboratory tests show that juvenile Slough crayfish were more secretive and spent much more time in aquatic vegetation than did juvenile Everglades crayfish, during both day and night (VanArman 2003). Related growth studies under similar laboratory conditions indicated that juvenile Slough crayfish of a given age were all similar in size to one another. By contrast, Everglades juveniles at the same age were size-structured, i.e. showed a wide range sizes (VanArman 2003).

Despite the key role that crayfish play in Everglades ecology and food webs, research on the specific roles of Everglades and Slough crayfish as predator and prey is lacking. The trophic role of crayfish as intermediates in food webs is highly important, however, the specific function of epigean crayfish in energy transfers has rarely been studied in Everglades wetlands. Studies that have focused on biology or ecology of either species (Rhoads 1970, 1976; Conover and Reid 1972; Kushlan and Kushlan 1979; Jordan 1996; Jordan et al. 1996; Hendrix 2000; Hendrix and Loftus 2000; Huffman 2001; VanArman 2003; Dorn and Trexler 2006) may mention trophic relationships, but often base these associations on presumed links derived from research conducted on other crayfish species or in locations other than south Florida. **Figure 8** shows a conceptual model of the role played by Everglades and Slough crayfish, as keystone species in Everglades food webs. This model is an attempt to expand elements shown in the ecological model of the Everglades presented by Ogden (2005) and includes observed (documented in scientific literature) and presumed relationships.

Habitat:

In much of the Everglades literature, only one species was found in a specific type of habitat (Hobbs 1942; Kushlan and Kushlan 1979; Jordan 1996). In fact, before 2000 it was assumed by all researchers that the Everglades crayfish was the only epigean crayfish inhabiting Everglades wetlands. The presence of Slough crayfish actually was noted in 1942 (Hobbs) in water conservation area 1 in Palm Beach County, and in 1985 (Rudolph) in Broward County canals, but their presence in Everglades wetlands was not widely recognized until 2000 (Hendrix 2000; Hendrix and Loftus 2000). At that time, Hendrix and Loftus (2000) noted that Everglades crayfish prefer short hydroperiod, shallower waters, whereas Slough crayfish prefer more permanent, deeper waters. VanArman (2003) noted that during crayfish collections, each species was usually found within its corresponding habitat type as noted by Hendrix and Loftus. However, Everglades and Slough crayfish were occasionally found in syntopic distribution (share the same habitats within the same geographic range) in Everglades environments (Hendrix and Loftus 2000) and in the Corbett area (VanArman 2003). Although there may be replacement of species seasonally in some locations, it could be assumed that resource partitioning is taking place, at least at the time of the collections.

Obtaining and processing nutrients are major driving forces in the success of any population. Slough crayfish generally prefer to live in permanent bodies of water where food from vegetation and aquatic animals is present year round. Everglades crayfish, on the other hand, often change locations seasonally, through a variety of habitats, burrow to the water table, and are known to migrate over land.

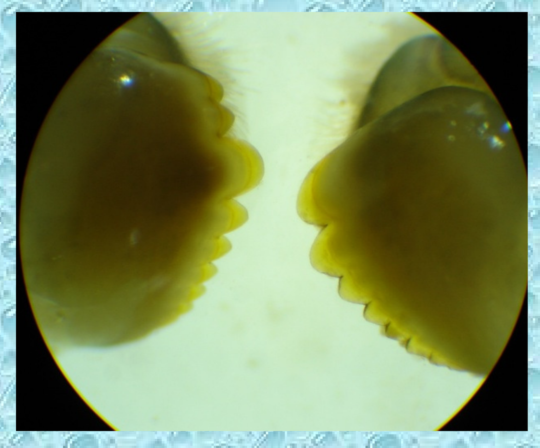

Figure 7a. Pa Mandibles

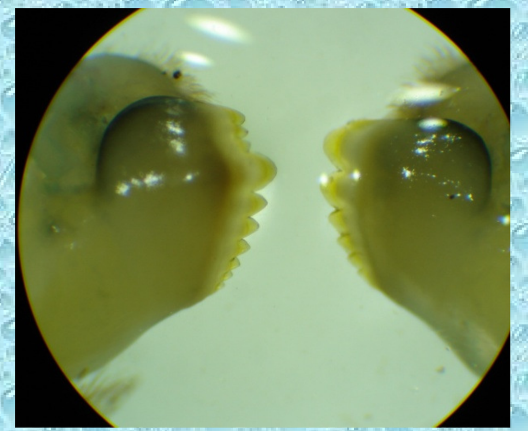

Figure 7b. Pf Mandibles

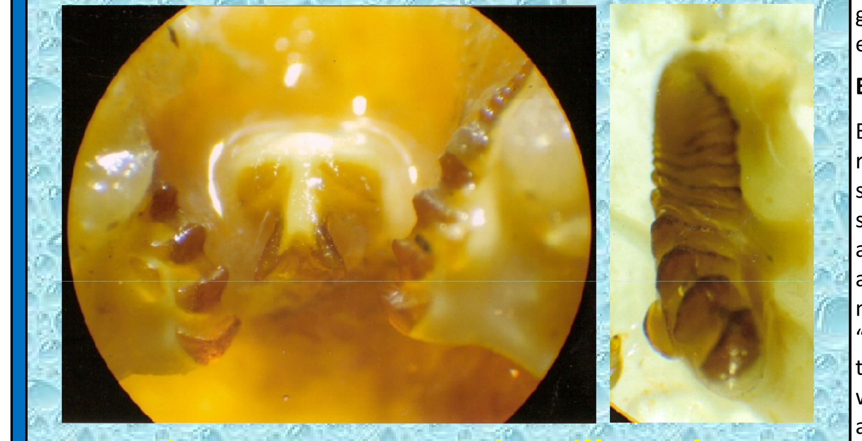

Figure 7c. Pa Gastric Mill Teeth and Right Lateral Tooth

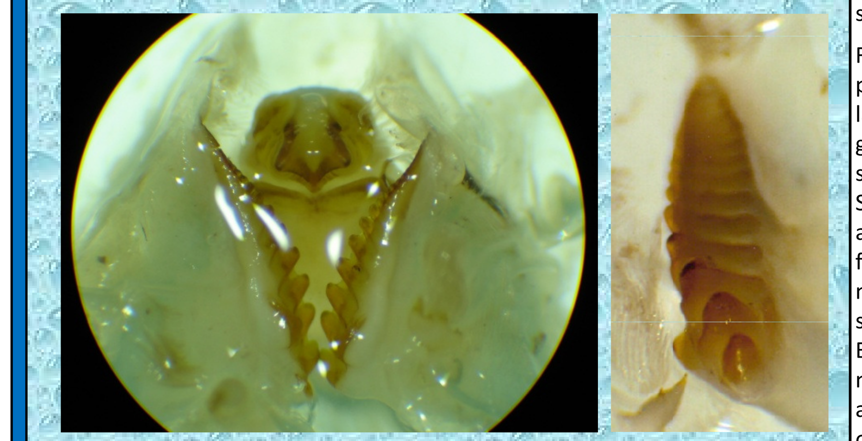

Figure 7d. Pf Gastric Mill Teeth and Right Lateral Tooth

Discussion (Cont.)

The ATLSS SESI model (Loftus et al. 2003) indicates that Everglades crayfish could live in more complex habitats that provide a greater variety of food sources than Slough crayfish. Although both species can be classified as opportunistic omnivores, the behavior and size-structured growth characteristics of Everglades crayfish may account for differences in feeding structures.

Mandibles:

A number of previous studies of crustacean masticatory structures have focused on mandibles and gastric mill complexes. The function of the mandible varies with diet and may be used to bite and cut or tear food, such as plant materials and animal prey, rendering pieces small enough for digestion, or may merely aid in pressing material into the esophagus with the aid of other appendages (Caine 1975a; Bouchard 1977). The blade-like incisor region is useful as a scraping tool, especially for obtaining aufwuchs in lentic environments where vegetation is abundant (Bouchard 1977). Crayfish mandibles are not efficient for chewing, but the remnants are further processed by the teeth of the gastric mill in the cardiac stomach (Caine 1975; Bouchard 1977).

Morphological features of the masticatory surfaces may indicate phylogenetic relationships among species, as well as a relationship to food sources (Bouchard 1977). The mandibles of most procambarid crayfish species have similar general structure (Caine 1975a). Everglades crayfish have slightly larger mandibles than slough crayfish (although this difference was not statistically significant for sample size used in this experiment) and significantly fewer mandibular teeth. These differences suggest that Everglades crayfish teeth may be slightly larger and better adapted to processing a greater diversity of food types. Additional, more detailed, studies may be warranted to examine the relative sizes of individual teeth on the mandibles.

Gastric mill complex (median and lateral teeth):

Caine (1975a, b) and Bouchard (1977) give riveting and thorough accounts of the masticating process in the gastric mill. Caine hypothesized that because there was little difference between mandibles in cambarids, that there would be a difference in the structure of the gastric mill complex within members of the genus *Procambarus.* The gastric mill consists of a median tooth with a dorsal projection (on the mesocardiac ossicle) and two lateral teeth (Caine 1975a, b; Chiska and Kozaka 2003). As food moves through the cardiac stomach by peristaltic waves, larger material is cut and crushed by the medially moving lateral teeth and ventrally moving median tooth complex. More robust gastric mills allow consumption of larger and harder prey (Suthers and Anderson 1981). A small dorsal tooth would show a minor role in feeding, perhaps simply to push food against lateral plates

Gastric mills in epigean (living above-ground) species of *Procambarus* appear similar in structure, including four species studied by Caine (1975a) , *P. clarkii* (Chiska and Kozaka. 2003), and Everglades and Slough crayfish (this study). The median tooth on the Everglades crayfish was longer and the "Y" shaped horns appeared more pointed than those of Slough crayfish. Caine (1975a,b) found that the structure of the gastric mill was influenced by both diet and phylogeny, but the effect of diet seems to be more important .

Lateral teeth:

The lateral teeth include molar-like (used for grinding) and incisor-like processes (used for biting and shredding). Comparisons of types of teeth in procambarids showed that there were four incisors on lateral teeth of the four epigean species from northwest Florida (Caine (1975a) and three to four incisors on *P. clarkii* lateral teeth (Chiska and Kozaka 2003). Everglades and Slough crayfish each showed three to four incisors. The remainder of the teeth were ridged molars. Within individual crayfish, both right and left lateral teeth contain the same number of teeth and are similar in structure. As the crayfish grows closer to shedding the lateral teeth become worn; new molts have sharper lateral teeth. These changes in morphology, due to stage in the molt cycle, make it more difficult to interpret differences in size and shape of teeth as a basis to distinguish between species. The presence of more teeth on the Slough crayfish lateral tooth suggests that this species may be better able to grind food to a smaller particle size and thus digest some food more efficiently.

Ecological implications:

Epigean procambarids are opportunistic omnivores that can use a wide range of macro-food resources. The primary masticating structures are similar, large, and complex in epigean crayfish, including the four species studied by Caine (1975a), *P. clarkii (*Chiska and Kozaka 2003), and *P. alleni* and *P. fallax* (this study). The greatest differences in gastric mills are associated with diet (Schaeffer 1970; Caine 1975a, b; Woods 1995). The more complex the median tooth of the gastric mill, and its bifurcated "wings", the more crushing power it has against the apposition of lateral teeth, and the less suited to feeding on detritus (Caine 1975a, b). Animals with simpler gastric mill structures, such as median and lateral teeth that are reduced in size and sharpness, would experience a decrease in grinding surfaces, and probably feed on organic silt in natural habitats. The small grinding teeth on lateral teeth in silt feeders are aided by sand and shell fragments (Suthers 1984), none of which were noted in stomachs of Everglades and Slough crayfish.

Feeding structures may indicate phylogenetic relationships within procambarids. Mandibles and the gastric mill complex (median and lateral teeth) of Everglades and Slough crayfish appear similar. The greater number of teeth on mandibles (used for cutting, tearing, and scraping of food) and lateral teeth of the gastric mill (used for grinding) of Slough crayfish could provide an advantage for consuming vegetation as a larger part of the diet. The significantly larger gastric mill median tooth, found on Everglades crayfish, could provide a greater surface for mastication of chitinous exoskeletons of other arthropods, thin mollusk shells, and larger animal material for a species that is more carnivorous. Even though the larger lateral teeth of Everglades crayfish have fewer molars, the teeth might be larger and the increased surface area would also allow grinding of vegetation, possibly composed of a greater variety of textures, than those plants used by Slough crayfish.

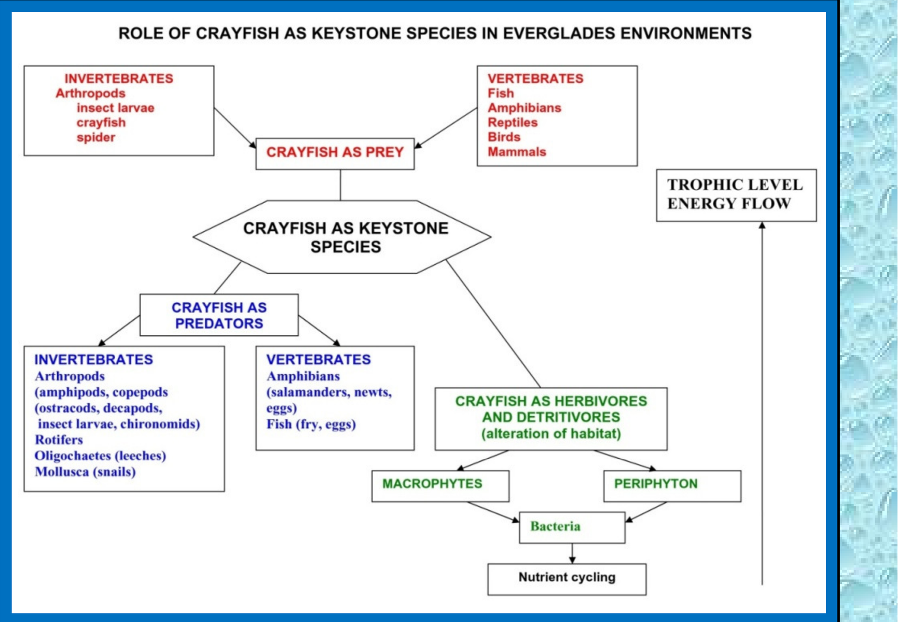

Figure 8. Conceptual Model of Role of Crayfish in the Everglades.

Summary and Conclusions

Small, but significant differences of feeding structures between Everglades and Slough crayfish could account for some differences in utilization of microhabitat resources. When combined with habitat preferences, and behavioral and developmental differences between these two species, the result may be that they are not in direct competition for resources, even though they occupy the same area.

Everglades Crayfish:

- Everglades crayfish generally prefer short hydroperiods and temporary wetlands.
- Everglades crayfish have a greater tendency to migrate over land and dig burrows in response to seasonal changes in the environment.
- Everglades crayfish may have size-structured populations and are more aggressive than Slough crayfish.
- As opportunistic omnivores with slightly larger gastric mill median and lateral teeth, they could obtain and utilize a greater variety of food sources and perhaps consume larger particles than Slough crayfish.

Slough Crayfish

- Slough crayfish prefer long hydroperiods, more permanent bodies of water with abundant vegetation, probably year round.
- This species prefers to live in permanent water bodies with more stable food sources (plants and animals), and therefore is less adapted to the perils of changing locations seasonally in order to locate food and water.
- The population is less size-structured, individuals are less aggressive and tend to hide in vegetation more, both night and day, than Everglades crayfish.
- Slough crayfish can also be classified as opportunistic omnivores; however, they have more mandibular and lateral teeth (molars), and hence more surface area for grinding and masticating vegetation.

Implications for Everglades Restoration

- Research on crayfish in Everglades environments has focused primarily on hydrologic effects on crayfish; little work has been conducted on biology.
- Of special concern for crayfish is the effect of hydrological changes on microhabitats and the composition of flora and fauna in affected habitats.
- The ability of these two crayfish species to coexist in the Everglades and to even occur within the same habitat, seems to depend primarily on differences in reproductive strategies, growth rates, behavior, which result in a degree of resource partitioning. Subtle differences in feeding apparatus may also contribute to this partitioning.
- Relatively subtle microhabitat changes on flora and fauna could dramatically influence food availability for particular crayfish species and thus their ability to function as predators and prey in the ecosystem.

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